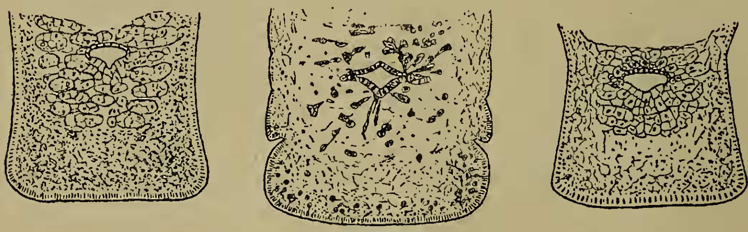
THE AFFINITIES OF *PYRAMIDULA*, *PATULASTRA*, *ACANTHINULA*, AND *VALLONIA*.

By Hugh Watson, M.A.

Read 12th December, 1919.

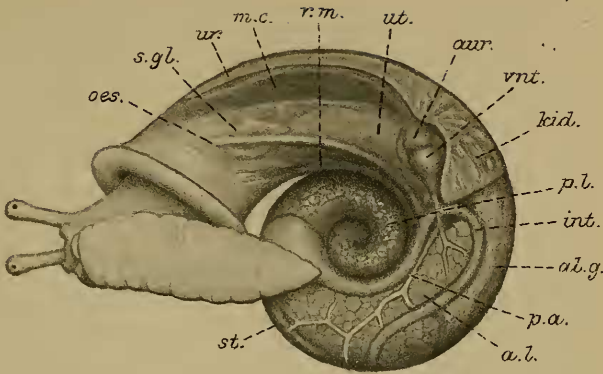
Introduction.—Much uncertainty seems to prevail about the true affinities of some of the smaller snails found in the British Isles. Thus, *Pyramidula rupestris* (Drap.) and *Patulastra balmei* (P. & M.)[1] —a species introduced into Ireland from the South of Europe— are commonly placed in the Endodontidæ; that is to say, in the same family as *Goniodiscus rotundatus* (Müll.), and even, as a rule, in the same genus. *Vallonia* and *Acanthinula*, on the other hand, are still often placed in the Helicidæ, between *Hygromia* and *Helicodonta*, although it is nearly twenty years since Dr. Pilsbry suggested that *Vallonia* should be removed from that family.[2] The chief purpose of the present article is to try to dispel this uncertainty, and to show that *Pyramidula*, *Patulastra*, *Acanthinula*, and *Vallonia* are fairly closely related to one another, but that these genera have very little affinity with either the Endodontidæ or the Helicidæ, their nearest British allies being among the forms assigned to the Pupillidæ, Cochlicopidæ, and Enidæ.



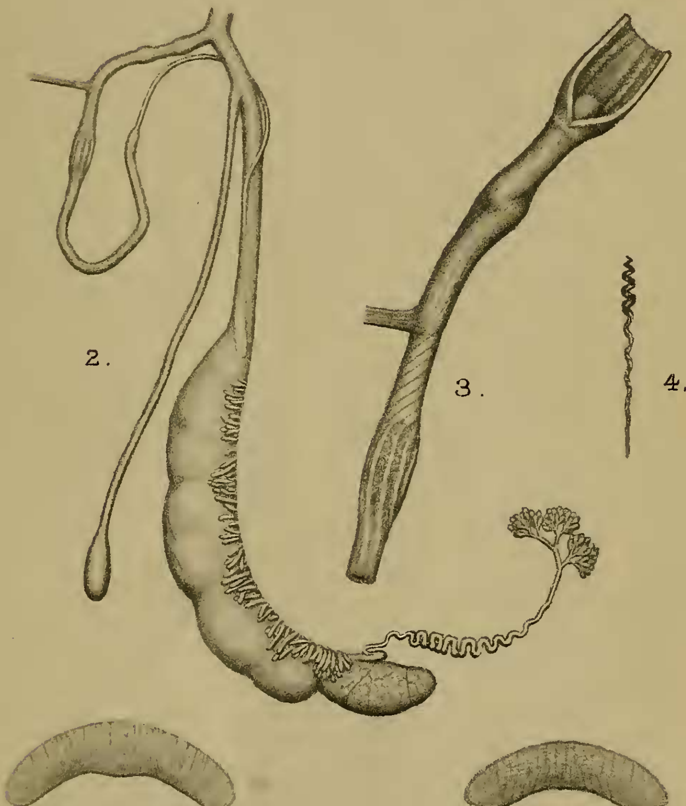
Figs. 1*a*–*c*.—Transverse sections through the foot of *Pyramidula*, *Goniodiscus*, and *Acanthinula*; showing the structure of the pedal gland, the presence or absence of peripodial grooves, etc.

The compilation of this paper has been greatly facilitated by the kindness of Dr. A. E. Boycott, who has allowed me to study his beautiful serial sections of *Acanthinula* and of several other small British snails. I am much indebted to Mr. A. W. Stelfox for preserved specimens of *Patulastra balmei* (P. & M.) and *Helicodiscus lineatus* (Say) from Ireland, and to Mr. W. E. Alkins for some living examples of *Vallonia excentrica* from Staffordshire. My thanks are also due to Dr. Boycott and Mr. B. B. Woodward for the loan of

[1] = *P. flavida* (Ziegler); see *Man. Conch.* (2nd ser.), vol. iii, 1887, p. 30.
[2] Proc. Acad. Nat. Sci. Phila., 1900, p. 564.



1.



2. 3. 4. 5. 6.

Anatomy of *Vallonia excentrica* (Figs. 1 & 6) & *Patulastra balmei* (Figs. 2–5).

reprints of three foreign papers which I was unable to consult in Cambridge.

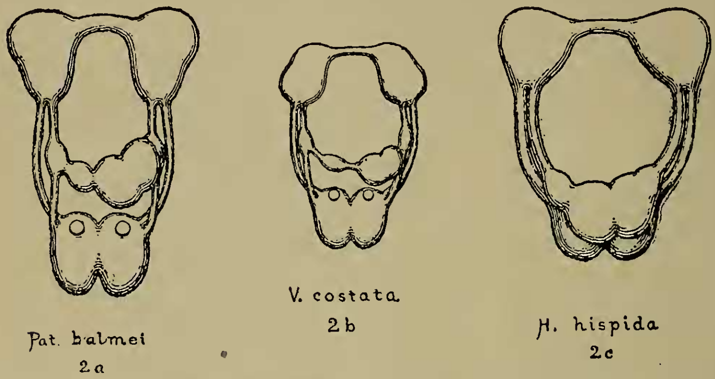
Evidence of the Foot.—A mere examination of the outside of the foot of *Pyramidula rupestris* and of *Patulastra balmei* is enough to show that these species cannot be closely allied to *Goniodiscus rotundatus* or *Helicodiscus lineatus*, or, indeed, to any form rightly assigned to the family Endodontidæ as defined by Pilsbry;[1] for both these species resemble *Acanthinula* and *Vallonia* in having no peripodial grooves. The striking nature of this difference between *Goniodiscus* on the one hand, and *Pyramidula* and *Acanthinula* on the other, may be seen from text-fig. 1. This figure also shows that *Pyramidula rupestris* resembles *Acanthinula* much more closely than *Goniodiscus* in the structure of its pedal gland, and the same is true of *Vallonia*. Further, the type of pedal gland that is found in *Acanthinula*, *Vallonia*, and *Pyramidula* occurs also in the Pupillidæ and the Cochlicopidæ, and these families are also without peripodial grooves. We see, therefore, that the evidence of the foot strongly supports the view that these three genera are all more nearly related to the Pupillidæ and the Cochlicopidæ than to the Endodontidæ.

Evidence of the Size.—The Helicidæ, however, are also without peripodial grooves. But in this family the dorsal wall of the duct of the pedal gland is longitudinally folded,[2] which is not the case in *Acanthinula*, *Vallonia*, or *Pyramidula*. Moreover, the very small size of these snails at least suggests that they may not be rightly assigned to the Helicidæ. It is true that the Rev. E. W. Bowell has expressed the opinion that size "has counted for too much in our systems of classification".[3] But he goes on to point out that an increase or diminution of size in an organism necessitates a redistribution of symmetry, because the constituent cells do not change their size proportionately, and that this rearrangement often involves a considerable morphological change. It would therefore seem improbable that a very great alteration in size could be easily and quickly effected in the course of evolution; and, if this be the case, the species of *Vallonia* and *Acanthinula* are not likely to be very closely related to *Helix pomatia* and its allies.

Evidence of the Central Nervous System.—Most students of comparative anatomy, however, would attach more weight to evidence afforded by the central nervous system than to mere considerations of size. Now the central nervous system in the Helicidæ is characterized not only by the close aggregation of the pedal, pleural, and visceral ganglia, but by the fact that the abdominal ganglion is completely united with the left parietal ganglion (see text-fig. 2*c*). Very different is the central nervous system of *Vallonia*, *Acanthinula*, *Patulastra*, and *Pyramidula*. In these

1 *Man. Conch.* (2nd ser.), vol. ix, 1894, p. xxviii.
2 André, Rev. Suisse de Zool., vol. ii, 1894, p. 298, pl. xii, fig. 5.
3 Proc. Malac. Soc. Lond., vol. viii, 1909, p. 379.

genera the ventral ganglia are much less closely aggregated, the pedal ganglia being some distance from the others, and the abdominal ganglion, instead of having become merged into the right parietal ganglion, is more or less united with the left. Text-fig. 2*b* shows the arrangement of these ganglia in the three British species of *Vallonia*, which do not differ appreciably from one another in their nervous system.[1] The central nervous system in *Pyramidula rupestris* and in both species of *Acanthinula* is almost identical with that in *Vallonia*. In *Patulastra balmei* (text-fig. 2*a*) the visceral loop is somewhat shorter, showing a tendency towards a greater concentration of the ganglia, but the nervous system remains of essentially the same type, that is to say, of a type quite different from that found in *Helix*,



FIGS. 2*a–c*.—Central nervous system of *Patulastra*, *Vallonia*, and *Hygromia*. The buccal ganglia, commissure, and connectives, which are of the usual type in all these genera, are omitted. (The figure of the nervous system of *Vallonia costata* might equally well represent that of *V. pulchella* or *V. excentrica*.)

but identical with that occurring in such forms as *Lauria cylindracea*, *Vertigo moulinsiana* and *V. antivertigo*, *Cochlicopa lubrica*, and *Ena obscura*. It is true that a similar arrangement of the ventral group of ganglia also occurs in the Endodontidæ, and that the abdominal ganglion of *Goniodiscus rotundatus*, for example, tends to be united with the right parietal ganglion and not with the left. But we have already seen that the deep peripodial grooves which characterize the Endodontidæ do not occur in *Pyramidula*, *Patulastra*, *Acanthinula*, or *Vallonia*.

EVIDENCE OF THE EXCRETORY SYSTEM.—Perhaps the most striking evidence of the true affinities of these four genera is that afforded by the course of the ureter.

[1] Sterki states (Proc. Acad. Nat. Sci. Phila., 1893, p. 237) that "in *V. parvula* (and other species) the cervical masses are adjacent to each other in nearly their entire length"; but this is very far from being the case in, at least, the British members of the genus.

The researches of Simroth,[1] Pilsbry,[2] and others have shown that the Stylommatophora may be divided according to the characters of the excretory system into four main groups, the Sigmurethra, the Orthurethra, the Heterurethra, and the Clasturethra, the great majority of the families belonging to the first two of these groups. In the Sigmurethra, to which both the Endodontidæ and the Helicidæ belong, the ureter arises from the front end of the kidney, runs back along its upper edge, and then bends round at the hind end of the mantle-cavity and passes forward immediately beneath the rectum, until it reaches the region of the respiratory opening. The first part, running backwards beside the kidney, is generally known as the primary ureter ; and the second part, that runs beside the rectum, as the secondary ureter. In a few of the most primitive members of the Sigmurethra the ureter throughout its length merely consists of a shallow open groove; and in many other genera, while the primary ureter takes the form of a closed duct, the secondary ureter remains open. But in most of the more highly organized snails both parts of the ureter are closed throughout, and this is the case in *Goniodiscus rotundatus*, as will be seen from text-fig. 3*c*. This species is clearly a typical member of the Sigmurethra.

In the Orthurethra, a group which includes the Pupillidæ, Cochlicopidæ, and Enidæ, the ureter follows a quite different course, for it passes straight forward from the front end of the kidney, parallel to the rectum but some distance below it. Just before reaching the mantle-edge the ureter terminates, its end being slightly bent upwards, and the opening being on the dorsal side of the extremity. From this point there runs backwards, along the upper side of the ureter, a shallow groove in the roof of the mantle-cavity, lined by an epithelium similar in character to that which lines the ureter itself. Now this description applies in every detail to the excretory system of *Pyramidula rupestris*, *Patulastra balmei*, *Acanthinula lamellata*, and the three species of *Vallonia* ; that is to say, these forms all belong to the Orthurethra. In *Vallonia* the kidney and ureter are relatively shorter than in *Patulastra* or *Pyramidula*, as will be seen on comparing text-figs. 3*a* and 3*b*;[3] but this is not an important difference, and is probably due to the whorls being fewer in number and the mantle-cavity shorter in consequence.

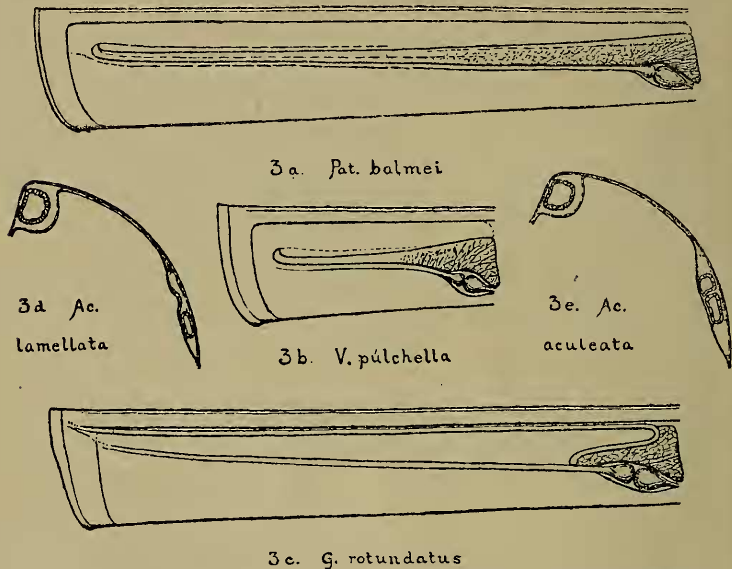
In *Acanthinula aculeata* we find a very interesting modification of the orthurethrous type. In this species the groove that runs backwards along the upper side of the ureter from its anterior opening has been converted into a closed duct ; and the actual

[1] Semper's *Reis. in Arch. Philip.*, iii, 1894, p. 70 ; Bronn's *Tier-Reich*, vol. iii, 1911, pp. 374–437.

[2] Proc. Acad. Nat. Sci. Phila., 1900, p. 561 ; *Man. Conch.* (2nd ser.), vol. xx, 1910, p. vii.

[3] See also pl. I, fig. 1, and pl. II, fig. 3.

opening of the ureter into the mantle-cavity is therefore just above the front end of the kidney, instead of near the mantle-edge. (Compare text-fig. 3*d*, which shows the condition in *Pyramidula*, *Patulastra*, *Vallonia*, and *Acanthinula lamellata*, with text-fig. 3*e*, which depicts a section through the roof of the mantle-cavity in *A. aculeata*.) Thus we might perhaps say that *A. aculeata* has a primary ureter running forwards leading into a secondary ureter running backwards, which is exactly the opposite arrangement to that found in sigmurethrous forms like *Goniodiscus rotundatus*, where the primary ureter runs backwards and the secondary ureter runs forwards.



FIGS. 3*a*–*e*.—Excretory organs of *Patulastra*, *Vallonia*, *Acanthinula*, and *Goniodiscus*. Figs. 3*a*, 3*b*, and 3*c* show the kidney, ureter, and other pallial organs, as seen from the outside, after the removal of the shell. Figs. 3*d* and 3*e* depict transverse sections of the roof of the mantle-cavity in front of the kidney, showing the ureter in section on the right and the rectum on the left.

The evidence of the excretory system, therefore, shows conclusively that none of the genera *Pyramidula*, *Patulastra*, *Vallonia*, and *Acanthinula* should be placed in or near the Endodontidæ or the Helicidæ, as they all belong to the Orthurethra. Indeed, it was apparently on these grounds alone that Pilsbry in 1900 suggested removing *Vallonia* from the Helicidæ and placing it in the Orthurethra in a new family.[1] For while very little has hitherto

[1] *Loc. cit.*

been published about the excretory system of *Pyramidula*, *Patulastra*, and *Acanthinula*,[1] it has been known for thirty years that the ureter in *Vallonia* was of a different type from that of *Helix*,[2] although the systematic importance of this difference was at first not generally realized.

EVIDENCE OF THE DIGESTIVE SYSTEM.—The jaw in *Pyramidula*, *Patulastra*, *Acanthinula*, *and Vallonia* is rather commonplace (pl. I, figs. 5 and 6).[3] It is thin—extremely so in *Pyramidula rupestris*—sometimes with a slight median projection, and crossed by a variable number of weak inconspicuous folds. It is usually furnished with a faint, ill-defined, backward extension, more or less divided into a number of small polygonal areas. Precisely the same type of jaw is found in the Pupillidæ, Enidæ, Cochlicopidæ, and some other Orthurethra, but as jaws of a similar kind are also commonly found in various sigmurethrous families, such as the Endodontidæ, Clausiliidæ, and Achatinidæ, not much importance can be attached to the evidence of this organ.

The radulæ of these genera are much more interesting. The Rev. E. W. Bowell has already published in these Proceedings figures of the radulæ of *Acanthinula aculeata* and *A. lamellata*, of *Vallonia costata* and *V. excentrica*, and of *Pyramidula rupestris*, as well as of *Goniodiscus rotundatus* and *Punctum pygmæum*.[4] I am therefore only portraying the radulæ of *Vallonia pulchella* and *Patulastra balmei*, the embryonic radulæ of the last species and *Pyramidula rupestris*, and the radula of *Helicodiscus lineatus* for comparison (text-figs. 4*a*–*e*).

The following are typical radular formulæ of the species with which this paper specially deals :—

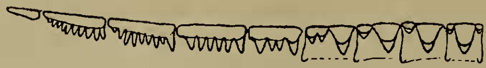
Pyramidula rupestris	(11 + 6 + 1 + 6 + 10) × 145
Acanthinula lamellata	(8 + 7 + 1 + 7 + 8) × 95
Acanthinula aculeata	(8 + 6 + 1 + 6 + 8) × 87
Vallonia costata	(9 + 5 + 1 + 5 + 9) × 70
Vallonia pulchella	(9 + 4 + 1 + 4 + 9) × 70
Vallonia excentrica	(9 + 4 + 1 + 4 + 9) × 76
Patulastra balmei	(17 + 9 + 1 + 9 + 17) × 125

[1] Hesse, however, quotes a brief but important note by Wiegmann, in which it is stated that *Pyramidula rupestris* has a remarkably elongated kidney, very different from that of *Goniodiscus rotundatus* or *G. ruderatus*, but resembling that of *Acanthinula aculeata*. (Nachr. Deutsch. Malak. Gesell., vol. xlvii, 1915, p. 57.)

[2] Behme, Archiv für Naturgeschichte, vol. i, 1889, pp. 5, 6.

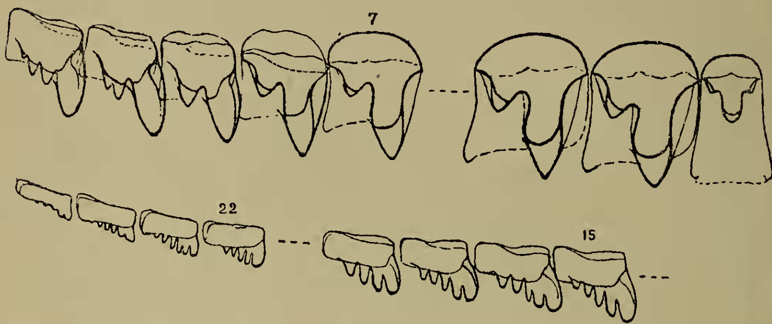
[3] Further figures of the jaw of *Vallonia* will be found in Sterki, Proc. Acad. Nat. Sci. Phila., 1893, pl. viii, figs. H, I, K, L, M, N, O, R; of *Acanthinula* in Lehmann, *Die lebenden Schnecken u. Muscheln der Umgegend Stettins u. in Pommern*, 1873, pl. x, fig. 25, pl. xi, fig. 32; and of *Pyramidula rupestris* in Taylor, *Monogr. L. & F.W. Moll. Brit. Is.*, vol. iii, 1909, p. 171, fig. 226 (fig. 227 on the same page evidently represents the radula of a very different species).

[4] Proc. Malac. Soc. Lond., vol. xi, 1914, pp. 158–61. Bowell has also figured the radula of *Pyramidula rupestris* in the Journal of Conchology, vol. xiv, 1915, p. 290.



4a. Pyramidula rupestris (embryo), ×1300

4b. Patulastra balmei (embryo), ×1000



4c. Patulastra balmei, ×750

4d. Vallonia pulchella, ×750

4e. Helicodiscus lineatus, ×750

FIGS. 4*a–e*.—Representative teeth from the radula of an embryo of *Pyramidula rupestris*, from Burnsall, Wharfedale; of a full-grown specimen of *Vallonia pulchella*, from Madingley, Cambridgeshire; and of embryonic and full-grown examples of *Patulastra balmei*, and a full-grown specimen of *Helicodiscus lineatus*, from the Glasnevin Botanic Gardens, Dublin.

Pyramidula rupestris usually has one more tooth on the left side of each row than on the right. *Patulastra balmei*, on the other hand, sometimes has one more tooth on the right side than on the left. In all three species of *Vallonia* there are often eight marginal teeth on each side, instead of nine. The number of transverse rows varies considerably.

The central tooth in *Pyramidula, Patulastra, Acanthinula,* and *Vallonia* is tricuspid, although the ectocones are usually very small. The whole tooth is also, as a rule, smaller than the laterals: in *Acanthinula aculeata, Patulastra balmei,* and all the species of *Vallonia,* it is very much smaller and narrower than the adjacent teeth; in *Acanthinula lamellata* it is also somewhat smaller; only in *Pyramidula* is it of about the same size as the laterals.

The lateral teeth in these genera are usually bicuspid, with quadrate bases, the outer posterior corners of the bases being more or less thickened, as is also the case in the central tooth. In *Pyramidula rupestris* the mesocones of both the central and lateral teeth are unusually broad, with very obtuse cusps, but this is probably an adaptation to the animal's special environment, for it would seem likely that broad rounded cusps would be best fitted for scraping the surface of the hard limestone walls and rocks on which this species generally lives. *Helicigona lapicida* is also very frequently found on limestone walls, and in this species the cusps of the central and lateral teeth have undergone a parallel modification, as Mr. Bowell has pointed out. In the embryonic radula of *Pyramidula rupestris* the broadening of these cusps is not quite so noticeable (text-fig. 4*a*), while in *P. humilis* (Hutton) it has not taken place at all (judging from a radula in the late Professor Gwatkin's collection). Excepting in *P. rupestris,* there is a decided gap between the mesocone and the ectocone of the lateral teeth, and in *Acanthinula lamellata* this gap is occupied by a small additional cusp, such as we also find in the genus *Vertigo*.[1] In *Vallonia,* and in the embryo of *Patulastra balmei,* the first lateral teeth are unusually large (text-figs. 4*b* and 4*d*).

The marginal teeth in *Pyramidula, Patulastra, Acanthinula,* and *Vallonia* are more numerous than the laterals, and are characteristically pectinate, having broad bases bearing a number of narrow cusps. The mesocone forms the first or innermost of these cusps. The remainder are smaller, excepting in *Pyramidula rupestris,* and are formed by the multiplication of the ectocone. No endocones are present in any of these genera.

Now, pectinate marginal teeth of this type do not occur in the Endodontidæ, nor in any other sigmurethrous family with which I am acquainted. It is true that in small snails of various types, and especially in those with narrow whorls, the outer marginal teeth tend

[1] See Bowell, Journ. of Conch., vol. xii, 1909, pl. v.

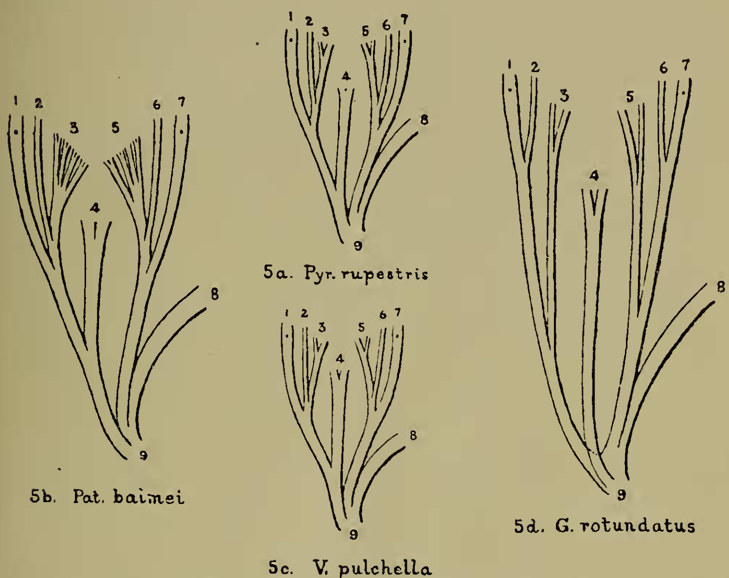
to become pectinate, the number of cusps being increased to compensate for the reduction in the number of separate teeth. But in the Sigmurethra the innermost cusp of these pectinate marginal teeth is formed by the endocone instead of the mesocone. This is the case, for example, in *Helicodiscus lineatus* (see text-fig. 4*e*), and in *Clausilia biplicata*, which has, perhaps, the most distinctly pectinate marginal teeth of our native Sigmurethra. In the Orthurethra, on the other hand, not only are pectinate teeth extremely common, but they are always of the type found in *Pyramidula*, *Patulastra*, *Acanthinula*, and *Vallonia*, that is to say, they are pectinate teeth without endocones. So far as I am aware, distinct endocones never occur in orthurethrous snails.

The marginal and lateral teeth of the four genera that we are considering are exceedingly like those occurring in many of the genera of the Pupillidæ, and they also greatly resemble those found in the Cochlicopidæ and Amastridæ; moreover, they only differ very slightly from those occurring in the less specialized members of the Enidæ. *Pyramidula* resembles the Pupillidæ in its central tooth being large; *Patulastra*, *Vallonia*, and *Acanthinula aculeata* agree with *Cochlicopa*, *Azeca*, and *Leptachatina*, in having small, narrow central teeth; while the intermediate size in the central of *Acanthinula lamellata* is what we also sometimes find in the Enidæ. In short, the type of radula found in *Pyramidula*, *Patulastra*, *Vallonia*, and *Acanthinula* differs from that found in any of the sigmurethrous families, but agrees very closely with that which characterizes the less specialized genera of the Orthurethra.

The remainder of the alimentary canal is of the ordinary type, and does not appear to present any features of much systematic importance. It may be worth mentioning, however, that the species of *Vallonia* and *Acanthinula* resemble *Cochlicopa lubrica* and *Ena obscura* in having the salivary glands united with each other below the œsophagus, and not above it—a rather unusual arrangement—and also that *Pyramidula rupestris* differs from *Patulastra balmei* and the three species of *Vallonia* in that the most posterior of the three lobes of the anterior division of the liver is without the dorsal extension which usually runs forward beside the suture, between the last part of the intestine and the albumen gland, in front of the stomach (compare pl. I, fig. 3, with Steenberg, Vidensk. Meddel. fra Dansk naturhist. Foren., vol. lxix, 1917, p. 12, fig. 7, *f*″).

Evidence of the Retractor Muscles.—It will be seen from text-figs. 5*a*–*d* that the branching of the columellar muscle is very similar in *Vallonia*, *Patulastra*, and *Pyramidula*; but that it is quite different in *Goniodiscus rotundatus*, particularly as regards the origin of the buccal retractor and the retractors of the lower tentacles. In such forms as *Lauria cylindracea*, *Ena obscura*, and *Cochlicopa lubrica*, however, the arrangement of these muscles is practically identical with that found in *Vallonia*, there being, apparently, very little variation in the muscular system of the Orthurethra. In all these snails the retractor of the right upper tentacle passes between the penis and the vagina. We see, then, that the evidence of the cephalic retractors supports that of the radula, excretory system, etc.

The penial retractor of *Vallonia* and *Patulastra* arises from the front end of the diaphragm, as in *Ena obscura* and *Cochlicopa lubrica*. In *Pyramidula* and *Acanthinula*,[1] on the other hand, it arises from the hinder end of the diaphragm, as it does in *Lauria cylindracea*.



FIGS. 5*a*–*d*.—Chief retractor muscles in *Pyramidula, Patulastra, Vallonia,* and *Goniodiscus*.

1. Retractor of left upper tentacle.
2. Retractor of left lower tentacle.
3. Retractor of lower part of left side of head and front end of foot.
4. Retractor of buccal mass.
5. Retractor of lower part of right side of head, genital atrium, and front end of foot.
6. Retractor of right lower tentacle.
7. Retractor of right upper tentacle.
8. Retractor of hinder part of foot.
9. Columellar muscle.

EVIDENCE OF THE REPRODUCTIVE SYSTEM. — Admirable descriptions and figures of the genital organs of the British species

[1] Steenberg states that in *Acanthinula aculeata* the penial retractor arises from the columellar muscle (*op. cit.*, p. 5); but Dr. Boycott's serial sections show that this is not the case in British specimens.

of *Acanthinula* have recently been published by Boycott[1] and Steenberg,[2] and the latter author has also dealt with the genital system of *Vallonia costata*;[3] while the details of the reproductive organs of *Patulastra balmei*, *Pyramidula rupestris*, and *Vallonia pulchella* will be seen from Plate I, figs. 2–4 and Plate II, figs. 1, 2, 4, 6. For the purpose of the present paper it will be enough to draw attention here to some of the more striking features of these organs.

In the first place we notice that in *Acanthinula aculeata* and *Vallonia costata* the penis has a long lateral appendix, swollen distally and also near its origin, where it receives one of the branches of the forked penial retractor. Now, a similar penial appendix occurs in most of the Orthurethra, namely in the Enidæ,[4] Amastridæ, and Achatinellidæ, in *Cochlicopa*, and in many of the Pupillidæ; and in the Enidæ,[5] Pupillidæ, and Achatinellidæ (excluding the Tornatellininæ), the penial retractor is also forked, and sends a branch to the enlarged basal portion of the appendix. On the other hand, a lateral penial appendix of this character is rarely found among any of the sigmurethrous families, although it seems to occur in the Sagdinæ,[6] a group of rather doubtful affinities.

A single specimen of *Vallonia costata* collected in November, 1919, at Little Shelford, Cambridgeshire, possessed a second appendix practically as long as the other, but without the basal enlargement, and arising from the anterior end of the penis (pl. II, fig. 5). Close to its terminal swelling this appendix was attached to the retractor of the right lower tentacle by a very slender muscle, and at about the same place it seemed to receive a small nerve from the right parietal ganglion. A second penial appendix, occupying a similar position, has also been found in a specimen of *Ena detrita*.[7]

In *Pyramidula rupestris* the penial appendix is much reduced, being represented by a mere knob (without muscular attachment), which occupies about the same position on the narrow penis as the appendix does in *Vallonia costata* (pl. II, fig. 4). It is easy to account for the reduction of the appendix in this species. *Pyramidula rupestris* is viviparous like so many of the Orthurethra, and the embryos before birth attain a relatively enormous size compared with the narrowness of the body-whorl of the parent: they do

[1] Journ. of Conch., vol. xv, 1917, p. 175; Proc. Malac. Soc. Lond., vol. xii, 1917, p. 221.

[2] *Op. cit.*, pp. 2. 6. [3] *Ibid.*, p. 9.

[4] Excepting in *Chondrula tridens* (see Moquin-Tandon, *Hist. Nat. Moll. France*, vol. ii, 1856, p. 298, pl. xxi, fig. 27; and Lehmann, *Die lebenden Schnecken u. Muscheln der Umgegend Stettins u. in Pommern*, 1873, p. 137, pl. xiii, fig. 46).

[5] Excepting in *Ena* (*Zebrina*) *detrita*. (See Beck, Jenaische Zeitschr. Naturw., vol. xlviii, 1912, pl. ix, fig. 25*a*.)

[6] Pilsbry, *Man. Conch.* (2nd ser.), vol. ix, 1894, pp. 59, 65, pl. xxi, figs. 9, 10; pl. xxxv, figs. 2, 3, 12.

[7] Beck, *op. cit.*, vol. xlviii, 1912, p. 230, text-fig. 23.

not leave any room for accessory organs that are not absolutely necessary.

Patulastra balmei is also viviparous, and in this species there seems to be no trace of a penial appendix, as is the case in the British species of *Azeca* and in many of the Pupillidæ. But the absence of an appendix is fully counterbalanced by the remarkable complexity of the internal structure of the epiphallus and penis (pl. I, fig. 3). A well-marked epiphallus is also developed in the other three genera that we are considering, and in *Acanthinula aculeata* it bears a couple of extremely short, thick flagella. These are very different from the slender flagellum of *Helix*—very unlike " little whips "—but similar flagella occur in some of the Enidæ and Pupillidæ.

We see, therefore, that *Pyramidula*, *Patulastra*, *Acanthinula*, and *Vallonia* agree closely with the Pupillidæ, Enidæ, and their allies in their male genital ducts—when these are present. Boycott and Steenberg, however, have shown that in all the specimens of *Acanthinula lamellata* that they examined, the penis, epiphallus, etc., were entirely absent, and Dr. Boycott found that the same was true of about half of the full-grown examples of *A. aculeata* that he studied. In both species the first part of the slender vas deferens is present beside the oviduct, but in these individuals it stops abruptly at about the level of the anterior end of the receptacular duct, and not a trace of the rest of the male organs exists. The physiological significance of this remarkable phenomenon has been so ably discussed by Dr. Boycott that I need not deal with it again. From a purely systematic point of view it is of more interest to point out that the same phenomenon occurs in *Vallonia*. I have made a very careful examination of the genital ducts of no fewer than 98 full-grown specimens of *Vallonia*, 45 being examples of *V. costata*, 31 of *V. pulchella*, and 22 of *V. excentrica*. All the examples of *V. pulchella*, and most of those of the other two species were collected in Cambridgeshire ; about half were examined in the spring, but 26 specimens of *V. costata*, 12 of *V. pulchella*, and 10 of *V. excentrica* not until November. Of all these specimens only three examples of *V. costata* had any male organs, two being found in November and the other one in the spring. In the remaining 95 individuals the female ducts were well developed, but there was no trace of the male ducts ; even the first part of the vas deferens could not be found, but the reproductive organs of all three species closely resembled pl. II, fig. 6. The fact that this unusual phenomenon occurs in both *Vallonia* and *Acanthinula* supports the view that these two genera are closely related to each other and to the Pupillidæ, for the same phenomenon occurs in at least one member of that family, namely, *Vertigo moulinsiana*.[1]

[1] It has been suggested that *Vertigo* should be placed in a separate family, since it has no lower tentacles (Kennard & Woodward, *List of British Non-Marine Mollusca*, 1914, p. 2) ; but in most respects the anatomy of this genus

Steenberg has drawn attention to the peculiar form of the prostate gland in *Acanthinula* and *Vallonia*.[1] In these genera it consists of a small number of moderately long tubules, situated at the posterior end of the common duct, just in front of the albumen gland (pl. II, fig. 5). It is, however, characteristic of the Orthurethra that the so-called prostate gland, instead of forming a compact ribbon extending along the whole of the common duct, consists of more distinctly separate tubules, which sometimes attain a considerable length, but tend to be chiefly concentrated towards the posterior end of the common duct, and are, as a rule, entirely confined to that end in the smaller species. Thus, in *Cochlicopa lubrica* and *Lauria cylindracea* we find the same type of prostate gland as in *Acanthinula* and *Vallonia.*

In *Patulastra balmei*, a much larger species than the others, the prostate gland consists of a large number of separate narrow tubules, forming an irregular fringe, which extends along almost the entire length of the common duct (pl. I, fig. 2). It thus resembles more closely the type of prostate gland found in the Enidæ. In *Pyramidula rupestris*, on the other hand, the gland is greatly reduced, and consists of a few extremely small and narrow tubules at the posterior end of the common duct (pl. II, fig. 4).

It is interesting to notice that although a prostate gland occurs in *Acanthinula lamellata* it is absent in those examples of *A. aculeata* that have no male ducts;[2] while in the similar specimens of *Vallonia* it is quite vestigial, being so small as to be only visible in stained preparations under the microscope (compare pl. II, figs. 5 and 6). On the other hand, in the British species of *Azeca*, in which the vas deferens is unusually broad in comparison with the size of the snail, the prostate gland attains relatively enormous dimensions. While, therefore, the function of this gland remains doubtful, it seems not unlikely that it produces a secretion which normally passes down the male ducts.

The receptacular duct is long in the genera that we are considering, especially in *Patulastra balmei* and *Acanthinula aculeata*, and it is unbranched. In this it resembles all the Orthurethra, excepting *Cochlicopa* and the Palæarctic Enidæ. The oviduct and vagina are without other appendages.

More than fifty years ago Goldfuss said that *Vallonia pulchella* and *V. costata* both possessed darts,[3] and in 1873 Lehmann stated that *Vallonia pulchella* had a dart-sac, and showed one in his figures of this species.[4] He also showed dart-sacs in his figures of *Acanthinula*

closely resembles that of the Pupillidæ, and I agree with Dr. Pilsbry in thinking that it should be retained in this family (*Man. Conch.* (2nd ser.), vol. xxv, 1919, pp. 68, 69).

[1] *Op. cit.*, p. 14.

[2] Boycott, Proc. Malac. Soc. Lond., vol. xii, 1917, p. 225.

[3] Verhandl. naturh. Verein. preuss. Rheinl. & Westphal., 1856, p. 52.

[4] *Op. cit.*, p. 92, pl. xi, fig. 30.

lamellata and *A. aculeata*, and depicted a couple of curved darts as belonging to the latter species, although he does not mention them in the text.[1] In 1884 Ashford described and figured a dart and dart-sac in *Vallonia pulchella*, stating that the dart was straight, acutely conical, and 0·2 mm. in length.[2] Ashford, however, said that his information concerning these organs was offered subject to confirmation or correction, as further examination was desirable; and Steenberg has recently denied the existence of a dart-sac and dart in *Vallonia* and *Acanthinula*.[3]

In all the examples of these snails that I have examined, I have never found a dart; yet I would hesitate to say positively that one is never developed, and that all the older authors were quite wrong. It seems extremely improbable that the vagina of *Vallonia* or *Acanthinula* could ever develop a dart-sac, but there is much to be said in favour of the view that the enlarged basal portion of the penial appendix of the Orthurethra is homologous with the dart-sac of the Sigmurethra.[4] The distance between the proximal end of the penial appendix and the genital atrium varies in the Orthurethra, and in some of the Enidæ the appendix seems to occupy exactly the position that the dart-sac holds in *Zonitoides* and many other members of the Zonitidæ.[5] Moreover, the dart-sac in the Zonitidæ often has no dart, and sometimes it may bear a long continuation, very like the rest of the penial appendix in the Orthurethra.[6] Now, if this homology be correct, it is quite conceivable that under certain circumstances *Vallonia*, and perhaps also *Acanthinula*, might possibly secrete a dart in the penial appendix; and as the older authors thought that these snails were Helices, if they did find a dart they might easily assume that the structure in which they found it must be a dart-sac of the type that usually occurs in the Helicidæ.

However this may be, it is clear that the evidence of the reproductive system, taken as a whole, supports that of the other organs which we have already considered. A classification that is based on the study of a single organ, or even of a single group of organs, is often unnatural, and should always be regarded with suspicion; but it is evident that those authors who have already transferred *Acanthinula* from the Helicidæ to the Orthurethra, on account of the form of the genital ducts, have undoubtedly acted rightly, and that not only *Vallonia*, but also *Pyramidula* and *Patulastra* must certainly be placed in the Orthurethra as well.

[1] *Ibid.*, pl. x, fig. 25, pl. xi, fig. 32.
[2] Journ. of Conch., vol. iv, p. 198, pl. viii, figs. 8, 9.
[3] *Op. cit.*, pp. 6, 8, 12, 13.
[4] See Simroth, Journ. Coll. Sci. Tokyo, vol. xii, 1898, p. 82.
[5] See, for example, Wiegmann's figure of *Pachnodus velutinus* (Pfr.) in Mitth. Zool. Samml. Mus. Berlin, vol. i, 1898, pl. iv, fig. 8.
[6] As in *Staffordia daflaensis* Godwin-Austen, *L. and F.W. Moll. of India*, vol. ii, 1907, pl. cxiii, figs. 1*h*, 1*i*.

For we have seen that whether we regard the locomotory or the nervous system, the excretory or the digestive system, the muscular or the reproductive system, all the evidence points to the same conclusion.

FAMILY RELATIONSHIPS OF *ACANTHINULA*, *VALLONIA*, *PATULASTRA*, AND *PYRAMIDULA*. While it is easy to be certain that these four genera belong to the Orthurethra, and have very little affinity with the Endodontidæ or the Helicidæ, in the present imperfect state of our knowledge it is very difficult to decide exactly where they should be placed among the various orthurethrous families.

Steenberg considers that *Acanthinula* and *Vallonia* are nearly allied to each other, and he places them provisionally in a family by themselves, which he names the Acanthinulidæ, and which he believes to be closely related to both the Enidæ and the Pupillidæ.[1] Now it is evident that *Vallonia* and *Acanthinula* are closely allied genera. It is true that *Acanthinula* differs from *Vallonia* in the higher spire, narrower umbilicus, and darker colour of its shell; in the smaller size and slightly larger number of the lateral teeth of the radula;[2] and also, when the male organs are developed, in the shortness of the part of the penis in front of the penial appendix, the presence of a pair of small flagella on the epiphallus, and the posterior origin of the penial retractor. These differences, however, while quite enough to establish beyond doubt the generic distinctness of *Vallonia* and *Acanthinula*, are not very much greater than those that separate *Acanthinula aculeata* and *A. lamellata*,[3] and would certainly not justify the placing of the two genera in separate families or even in separate sub-families.

That Steenberg is also right in regarding these genera as closely related to both the Enidæ and the Pupillidæ is abundantly clear from the evidence that has already been put forward in this article. But if the group which these genera form is to be regarded as a distinct family, it would seem better to call it the Valloniidæ rather than the Acanthinulidæ, inasmuch as the former name is not only shorter and derived from an older generic name, but has been in use for nearly twenty years,[4] whereas the name Acanthinulidæ is little more than two years old.

Patulastra differs widely from *Vallonia* and *Acanthinula* in its reproductive organs; and while the fact that it is viviparous might partly explain the absence of a penial appendix (as in *Pyramidula*[5]), this would not account for the complicated structure of the epiphallus

[1] Vidensk. Meddel. Dansk Naturh. Foren., vol. lxix, 1917, p. 14.

[2] The other differences in the radula are extremely slight, the rounded inner edges of the marginal teeth of *Acanthinula*, and the length of the central tooth of *A. aculeata*, being somewhat exaggerated in Bowell's figures (Proc. Malac. Soc. Lond., vol. xi, 1914, p. 158).

[3] See p. 29.

[4] Pilsbry, Proc. Acad. Nat. Sci. Phila., 1900, p. 564.

[5] See p. 16.

(pl. I, fig. 3), or the different character of the prostate gland (fig. 2). But the reproductive organs of *Patulastra* do not agree at all closely with those of any other genera with which I am acquainted, and in its radula (text-fig. 4*d*), as well as in most other features of its anatomy, it bears a strong resemblance to *Vallonia*. It would therefore seem best to assign *Patulastra* to the same family as *Vallonia* and *Acanthinula*, although it might perhaps be placed in a separate sub-family, unless any of the other foreign species of *Patulastra* should prove to have genital organs less unlike those of *Vallonia* and *Acanthinula* than are these organs in *P. balmei*.

Pyramidula differs from *Vallonia* and *Acanthinula* little, if any, more than does *Patulastra*, for while its radula is of a rather different type (text-fig. 4*a*), its reproductive organs are not quite so dissimilar (pl. II, fig. 4), and although it differs from *Vallonia* and *Patulastra* in the posterior origin of its penial retractor, it agrees in this respect with *Acanthinula*. The broad mesocones of the central and lateral teeth of *Pyramidula rupestris* may be due to its habitat (see p. 13), but this would not account for the larger central teeth, which are also possessed by *P. humilis* (Hutton). Now, similar central teeth are found in most of the Pupillidæ, and, apart from the broadened cusps of *P. rupestris*, the type of radula occurring in the genus *Pyramidula* agrees exactly with that usually found in that family. *Pyramidula* also closely resembles the Pupillidæ in its reproductive system, as well as in its central nervous system, pallial organs, retractor muscles, etc. Its black hermaphrodite duct resembles that of *Vertigo moulinsiana* and *V. antivertigo*, and the spirally coiled head of the spermatozoon (pl. II, fig. 1) agrees closely with that of *Lauria cylindracea*; while its exceedingly short lower tentacles also remind one of the Pupillidæ. Indeed, there seem to be no differences between *Pyramidula* and an ordinary member of the Pupillidæ, excepting in the form of the shell and the simplicity of its peristome.[1] But these differences in the shell disappear if we compare *Pyramidula*, not with a full-grown *Pupilla*, but with a young specimen, for many genera of the Pupillidæ have Heliciform umbilicate young, closely resembling the more conical varieties of *Pyramidula*. I would therefore suggest that *Pyramidula* is a member of the Pupillidæ in which the reproductive organs develop early, and the animal devotes its energies to providing its numerous offspring with well-developed shells before they are born, instead of completing its own shell.

A parallel case among British snails is found in *Balea perversa*. This species is also viviparous, and is very like a young *Clausilia*; it forms no clausium, and never completes its aperture in the elaborate manner which is characteristic of that genus. Yet, as

[1] Hesse, in a paper just received (Nachr. Deutsch. Malak. Gesell., 1918, p. 110), upholds similar views to mine, but the species he terms *Pyr. rupestris* seems to differ from that examined by Moquin-Tandon and myself.

Steenberg has shown,[1] it is not a primitive member of the Clausiliidæ, but a highly specialized form, allied to *Clausilia biblicata.* The only reasonable explanation of the characters of the shell of *Balea perversa* seems to be that this species is a *Clausilia* which has sacrificed the completion of its own shell in its efforts to provide adequate shells for its young. And it seems likely that the same explanation applies to *Pyramidula.* For in the bleak, rocky situations in which *Pyramidula rupestris* is so often found, it is obviously specially advisable that the young should come into the world adequately protected.

If *Pyramidula* is simply a kind of *Pupilla* that never grows up, it clearly must be placed in the Pupillidæ. But we have already seen that the genus *Pyramidula* does not differ much from *Acanthinula* and *Vallonia,* excepting for the larger central teeth of the radula. In *Acanthinula lamellata,* however, the central teeth are not very much smaller than the laterals, and they are no smaller in *A.* (*Zoogenites*) *harpa,* according to Morse.[2] This feature, therefore, cannot be said to separate the Valloniidæ from the Pupillidæ, and there seem to be no other anatomical differences. The Heliciform shell of the Valloniidæ is not an important difference, for, according to Pilsbry, more than half of the sub-families into which he divides the Pupillidæ contain Helicoid forms.[3] And although it is easy to attach too much weight to the " recapitulation theory ", the fact that so many of the Pupillidæ are Heliciform when young, even though they are not when full-grown, suggests the possibility that the spire of the ancestral form of the family may have been no higher than that of *Acanthinula,* for example. There is some reason to suppose that the Pupiform members of the Streptaxidæ may have been evolved from the Helicoid forms, and possibly the course of evolution in the Pupillidæ may have followed parallel lines. Moreover, certain recent authors have already placed *Acanthinula* in the Pupillidæ,[4] and if *Acanthinula* should be assigned to that family, so should *Vallonia.* In other words, the Valloniidæ should be reduced to the rank of a sub-family of the Pupillidæ, like the Vertigininæ, etc. *Patulastra* should probably be placed in the same sub-family as *Vallonia* and *Acanthinula* ; though possibly it would be better placed in a separate sub-family of the Pupillidæ, on account of its very different reproductive system.

But *Vallonia, Acanthinula,* and *Patulastra* seem also to be very closely related to the Enidæ. This is due to the fact that the Palæarctic Enidæ do not differ in any essential features from the

[1] *Anatomie des Clausilies Danoises* : Mindeskrift for J. Steenstrup, No. 29, 1914, pp. 39, 40, 43.

[2] Binney, *Terrest. Air-breathing Mollusks of the U.S.,* vol. v, 1878, p. 341, fig. 225.

[3] *Man. Conch.* (2nd ser.), vol. xxiv, 1918, p. x.

[4] *e.g.* Pilsbry, *ibid.* (same page) ; C. R. Boettger : Nachr. Deutsch. Malak. Gesell., vol. xli, 1909, p. 4 ; vol. xliii, 1911, p. 24.

Pupillidæ, and should in my opinion be united with the family, although forming another distinct sub-family within the Pupillidæ.[1] *Ena* agrees closely with the Pupillidæ in its nervous system, excretory organs, retractor muscles, etc. There is no constant difference between the shells of the two groups, as is shown, for example, by the want of agreement among conchologists as to whether *Leucochiloides* (or *Pupoides*) should be placed in the Pupillidæ or in the Enidæ. The radulæ are of the same type, the only difference being that which is usually found between the larger and smaller species of the same group, namely, a tendency for the number of the cusps and the breadth of the teeth to be reduced in most of the Palæarctic Enidæ, as compared with the smaller Pupillidæ. The reproductive organs also are similar in most respects. The prostate gland, it is true, is longer in the Enidæ than in the majority of the Pupillidæ, but it is not longer than in *Patulastra balmei* (pl. I, fig. 2). The only constant difference seems to be that in the Palæarctic Enidæ the receptacular duct bears a diverticulum. But this feature can hardly be considered a sufficient reason for regarding the Enidæ as an entirely distinct family, since we may find in a single family some genera with, and some without, such a diverticulum as, for example, in the Helicidæ. And this difference is far less than that which sometimes exists between the reproductive organs of different individuals of *Vallonia costata*, living together on the same hedge-bank.

Moreover, the southern forms (such as *Pachnodus*) that are usually placed in the Enidæ are without this diverticulum of the receptacular duct. But these southern genera differ from the Palæarctic Enidæ in other respects also. Thus, most of the teeth of the radula, instead of having their major axes practically in a line with one another, are placed more or less obliquely, so that the outer side of one tooth is in front of the inner side of the tooth next beyond. This character, which gives a strikingly different aspect to the radula in many of the southern forms, is entirely absent in the Palæarctic species. There can be little doubt, in fact, that *Pachnodus* and its allies should be placed in a separate sub-family from the Palæarctic forms, or perhaps even in a distinct family.

Cochlicopa is in many ways intermediate between the Valloniinæ and the Eninæ in its anatomy. The radula, with its small central teeth, is, on the whole, very like that of *Vallonia* and *Patulastra*. The prostate gland is chiefly confined to the posterior end of the common duct, as in *Vallonia*, *Acanthinula*, and the more typical members of the Pupillidæ, although a few tubules are developed further forward. On the other hand, the receptacular duct bears a diverticulum, as in the Eninæ, and the penial retractor is not

[1] Hesse is also of the opinion that the Enidæ and the Pupillidæ should be united in one family (Nachr. Deutsch. Malak. Gesell., vol. xlvii, 1915, p. 57).

forked, but is of the same type as in *Ena* (*Zebrina*) *detrita*.[1] In its other organs *Cochlicopa* agrees closely with both the Eninæ and the Valloniinæ, as well as with the more typical Pupillidæ. It therefore seems evident that the Cochlicopidæ should also be reduced to the rank of a sub-family of the Pupillidæ.

Azeca is generally admitted to be closely allied to *Cochlicopa*, which it resembles in its radula as well as in its pallial organs, etc. Yet in its reproductive system the British species of *Azeca* differs widely from *Cochlicopa*.[2] The receptacular duct is unbranched, but the free oviduct bears an appendiculum instead. The prostate gland is greatly developed, especially towards its hinder end, which extends backwards beyond the albumen gland. The vas deferens is unusually thick, and there is no penial appendix in the British form, although Saint-Simon states that one is present in *Azeca menkeana alzenensis*.[3] In view of these striking differences between the genital organs of *Cochlicopa* and *Azeca*, the latter genus might well be placed in a distinct sub-family by itself.

Leptachatina, *Amastra*, and the other genera that Pilsbry includes in the Amastridæ, have reproductive organs intermediate in character between those of *Cochlicopa* and *Azeca*.[4] They have the large prostate gland and unbranched receptacular duct of *Azeca*, but in other respects they agree exactly with *Cochlicopa*. The radula has small central teeth, and is of the same type that we find in *Cochlicopa*, *Azeca*, and the Valloniinæ, and so are the pallial organs. Further, the shell in some species of *Leptachatina*, the most primitive of these genera, is remarkably like that of *Cochlicopa*. Indeed, Pilsbry himself says that "so far as the groups are known, no character of importance separates *Cochlicopa* from *Leptachatina*".[5] He modified this statement later by saying that the Amastridæ could be distinguished from the European forms by one character, namely the prostate gland,[6] but we have seen that this is not so, as *Azeca* has a large prostate like the Amastridæ. Therefore, in the present state of our knowledge there would appear to be no justification whatever for placing *Cochlicopa* and *Azeca* in one family and *Leptachatina* and *Amastra* in another. I therefore consider that the Amastridæ might also be reduced to the rank of a sub-family of the Pupillidæ and placed next to the Cochlicopinæ and the Azecinæ.

[1] Beck, Jenaische Zeitschr. Naturw., vol. xlviii, 1912, pl. ix, fig. 25*a*. In most of the Eninæ the penial retractor is bifurcated, as in *Vallonia*, *Acanthinula*, etc.; but the fork varies in size, being very small in *E. obscura*, though larger in *E. montana*.

[2] See Boycott, Journ. of Conch., vol. xvi, 1919, p. 53.

[3] Annales de Malacologie, vol. i, 1870, p. 29.

[4] Excepting in regard to the radula, my knowledge of the anatomy of these snails from the Hawaiian Islands is derived almost entirely from Pilsbry's excellent account in the *Manual of Conchology* (2nd ser.), vol. xxiii, 1915, pp. 57–68, pls. xii–xvii, xx, and xxii.

[5] *Op. cit.*, vol. xix, 1908, p. 212.

[6] *Ibid.*, vol. xxiii, 1915, p. 62.

In some respects these snails from the Hawaiian Islands show a specially strong resemblance to the Valloniinæ. Thus the lateral and marginal teeth of the radula of some of the species are remarkably similar to those of *Patulastra balmei*, more like them than those of any European form that I have seen. And although the central teeth in *Amastra* itself are even smaller than in the European genera, this does not seem to be the case in *Leptachatina*. Again, while the shells of some of the Amastrinæ scarcely differ from *Cochlicopa*, we find every gradation from this form to shells that are even flatter and more openly umbilicate than *Patulastra* or *Vallonia*; and the apical spiral striæ of *Armsia* and *Thaanumia* (a sub-genus of *Leptachatina*) resemble those of *Vallonia costata* and *Acanthinula aculeata*.

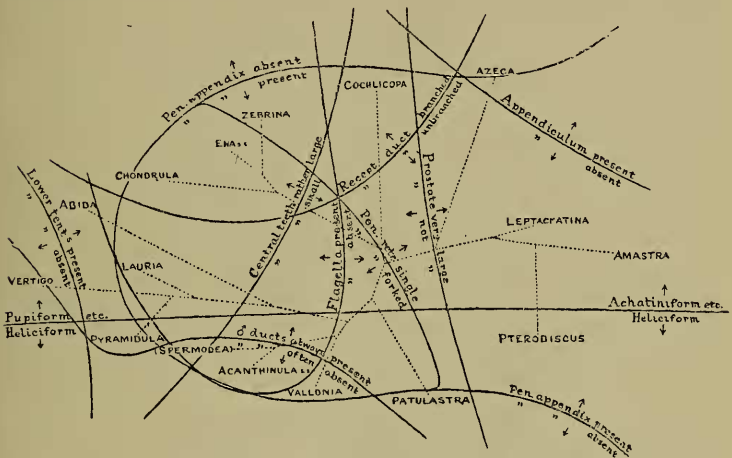


Diagram showing the diverse distribution of different characters among representative genera allied to the Pupillidæ, and illustrating the fact that a division of the group based on any single character would not accord with one based on any other. The dotted lines indicate one of the many possible views that might be held concerning the genetic connexions of the various genera.

We find, therefore, that although the sub-family Valloniinæ is undoubtedly closely related to the typical members of the Pupillidæ it is in many ways intermediate between the Pupillidæ, the Enidæ, the Cochlicopidæ, and the Amastridæ, agreeing closely with one group in one respect and with another in another respect, though resembling them all in most respects. It thus seems to help to link together these so-called families; to emphasize the fact that their supposed differences, when they exist at all, are scarcely to be compared with the differences that separate the families of the Sigmurethra, and to support the view that all these groups might well be united into a single family, divided into an unusually large number of sub-families. It is remarkable that the most striking differences that do occur within this family are often found among members of the same sub-family; as, for example, the difference between the shells of *Carelia* and *Planamastra*, between the radulæ of *Abida* and *Chondrina*, and between the genital organs of different individuals of *Acanthinula aculeata* or *Vallonia costata*.

It is not surprising that this family should have a wide distribution and a considerable variation in external form, seeing that it is the oldest known family of land snails. Shells generally assigned to the Pupillidæ—*Strophites grandæva*, Dawson, and *Dendropupa primæva* (Mathew)—have been found in the Upper Devonian strata of New Brunswick, and other species of the same genera occur in Carboniferous and Permian beds; and if the Upper Carboniferous shell from Nova Scotia, originally described as *Zonites* (*Conulus*) *priscus*, Carpenter, has been rightly regarded by modern authors as probably related to *Pyramidula*, it would seem that all the Palæozoic members of the Stylommatophora that have hitherto been discovered belong to this family.[1] This is a point of special interest, because the orthurethrous type of kidney is generally considered, on morphological grounds, to be more primitive and therefore, presumably, more ancient than the type found in the Sigmurethra, the group to which the majority of living snails belong.

The remaining families of the Orthurethra seem to be more distinct and less closely allied to *Pyramidula*, *Patulastra*, *Vallonia*, and *Acanthinula*. The family Achatinellidæ—in which I would include the Tornatellininæ as a very distinct sub-family—differs greatly from all the forms that we have been considering in its extraordinary radula, which resembles that of Athoracophoridæ. It is also characterized by its remarkably small albumen gland, while Pilsbry has pointed out that *Achatinella* differs from *Amastra* in other constant characters as well.[2] The Partulidæ is also a fairly distinct family, according to the same author's description.[3]

Glessula, which Pilsbry placed provisionally among the Orthurethra, is a sigmurethrous genus, very different from those with which we have been dealing, and it is not improbable that the same may prove to be true in the case of *Cæcilioides*, *Ferussacia*, and their allies. The radulæ of these genera are of the type found in the Achatinidæ, and differ widely from the types occurring in the Pupillidæ, Achatinellidæ, and Partulidæ.

On the other hand, it is possible that one or two other genera of small Heliciform snails, usually assigned to the Endodontidæ or the Helicidæ, should be placed in or near the Valloniinæ, in addition to those with which this article specially deals. Thus, *Aspasita*, which has generally been regarded as a section of *Helicodonta*, is

[1] B. B. Woodward, Proc Malac. Soc. Lond., vol. viii, 1908, pp. 73–7.
[2] *Op. cit.*, vol. xxiii, 1915, p. 61.
[3] *Ibid.*, vol. xx, 1909, pp. 155–60.

probably an orthurethrous genus allied to *Vallonia* and *Acanthinula*, judging from Hesse's preliminary description of *A. triaria*, Fr.,[1] and it has recently been placed in the Pupillidæ by Pilsbry.[2] It must not be supposed, however, that this is likely to be the case with many of the numerous small snails, chiefly found in the Southern Hemisphere, which Pilsbry placed in the Endodontidæ. For although the shells in some of these forms are very like *Patulastra* or *Acanthinula*, it is certain that in the great majority of cases this resemblance is purely superficial.

MUTUAL AFFINITIES OF THE BRITISH SPECIES OF *VALLONIA*.—The three forms of *Vallonia* that live in the British Isles are closely related to one another, and many collectors doubt whether they are specifically distinct.[3] Nevertheless, I think that Dr. Sterki was certainly right in regarding them as distinct species,[4] for each is distributed over a very wide area in Europe and America, they are sometimes found together, and yet they do not appear to merge into one another, but differ constantly in several characters. Perhaps the failure of many collectors to appreciate the specific differences is due partly to the minute size of these snails, but chiefly to the fact that comparative descriptions and figures of the three species have hitherto not been very accessible to English students.

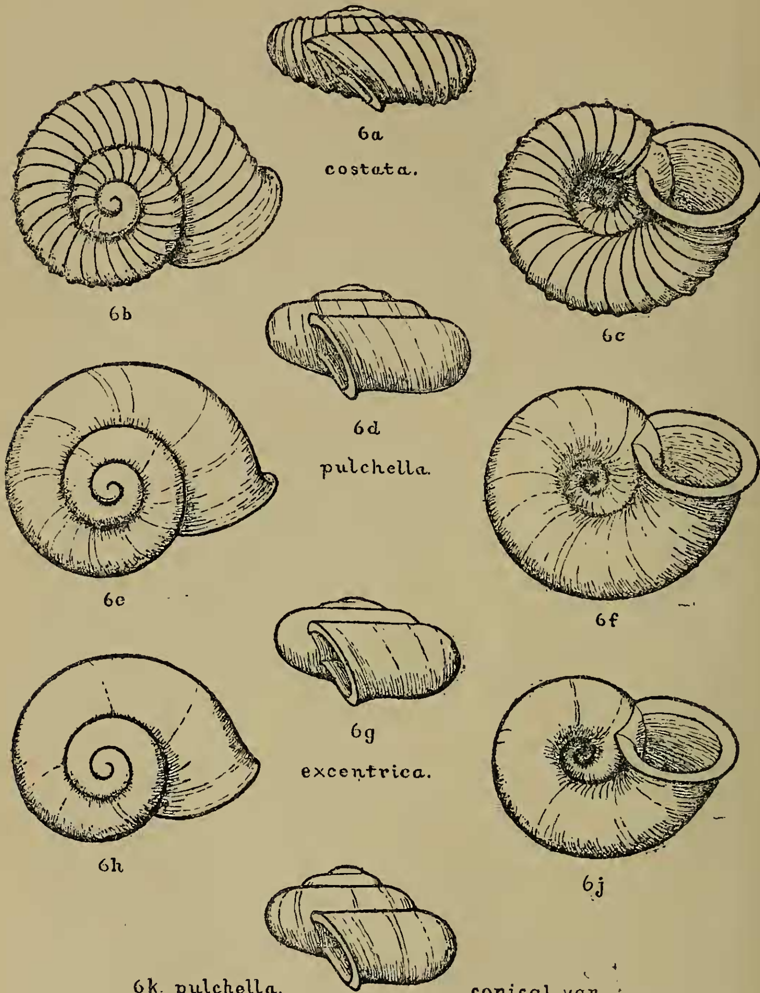
Vallonia costata is probably the most primitive of the three species, and should be placed first. It differs from the others not only in being furnished with conspicuous periostracal ribs, and in having more distinct microscopical spiral striæ on its protoconch, but also in the general form of the shell, and particularly in the deflection of the aperture (see text-fig. 6*a*). This last feature makes it easy to distinguish fossil specimens of this species, however worn they may be.

The radula of *Vallonia costata* differs from those of the other two British species in that the lateral teeth are five in number instead of four, the first being not quite so large as in *V. pulchella*, and their basal plates are more nearly square. Moreover, the marginal teeth usually have about five cusps, instead of six to eight, as in the other species.

This is perhaps the commonest species of *Vallonia* in England. It occurs with both the other species amongst grass, moss, etc., and also in drier situations, such as amongst ivy on the tops of walls, where it is frequently associated with *Lauria cylindracea*.

Vallonia pulchella is rather more local in its distribution, and seems to occur more often in damp situations. It appears to have

[1] Nachr. Deutsch. Malak. Gesell., vol. xlvii, 1915, p. 58.
[2] *Op. cit.*, vol. xxiv, 1918, p. x.
[3] *e.g.*, Cooper, Journ. of Conch., vol. xi, 1906, p. 340; Adams, *ibid.*, p. 364.
[4] See his excellent "Observations on *Vallonia*": Proc. Acad. Nat. Sci. Phila., 1893, pp. 234–79, pl. viii; as well as his shorter account of the genus in *Man. Conch.* (2nd series), vol. xiii, 1893, pp. 247–61, pls. xxxii, xxxiii.



FIGS. 6a–k.—Shells of the British species of *Vallonia*; all × 15. Figs. 6a–6j represent normal specimens of the three species from Cambridge. Fig. 6k depicts an unusually conical example of *V. pulchella* from Madingley, Cambridgeshire.

closer affinities with *V. costata* than has *V. excentrica*, and should therefore take the second place among the British species.

Text-fig. 6k depicts an unusually conical specimen of this species, found near the village of Madingley, in Cambridgeshire, associated with normal individuals of *V. pulchella*, a single specimen of *V. excentrica*, and a few examples of *V. costata*.